Polarization of marine light fields and animal orientation

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ABSTRACT

Animals in the sea absorb, scatter, reflect, emit and sense underwater light. Large well developed eyes in most long range marine migrators suggest its navigational importance. Submarine light polarization may provide species that perceive it with a kind of sun compass even in deep water. Laboratory evidence has been found for compass card-like orientation to e-vector direction by both fishes and crustaceans.

1. INTRODUCTION

Pelagic animals interact strongly with marine light even though they are not directly dependent, like phytoplankton, on photons as their source of energy. Absorption, reflection, scattering and emission of visible electromagnetic energy are, of course, widespread in marine animals. Consequently they may significantly modify not only the intrinsic optical properties of their medium but also its radiance distribution due primarily to penetrating light rays. The species involved as well as their size and developmental stages will determine the quality of such optical effects. Quantitatively organisms, considered as suspended particles, are usually allotted a mere trace role in marine optics. However, they are not uniformly distributed either in space or time and often occur in dense swarms which clearly will significantly affect underwater light. Consequently the overall number of animals involved and their state of aggregation will determine when and where such biological influences become important. Thus reproductive swarming and bioluminescent display, mass feeding and long range migration (both vertical and horizontal) may cause substantial daily, seasonal or geographical changes in local ocean optics. The relations involved show some parallels with underwater acoustics where animals as scatterers and emitters of sound significantly influence the presence and propagation of such pressure waves in the sea.

2. ANIMALS AND UNDERWATER LIGHT

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In view of these complex interactions, the optics and behavioral ecology of marine animals are proper adjuncts to the direct physical and geophysical study of ocean optics. More particularly the mechanisms that regulate animal migration, swarming and reproduction are of special relevance. Such controls are multiple, of course. Both internal genetic and physiological as well as external sensory factors contribute to the organism's clock and calendar as well as to their other navigational needs for a map and compass. The senses concerned fall into six operational categories depending on the kinds of environmental signals available: photic, mechanical, thermal, chemical, electric and magnetic. For present purposes the first of these is our main focal point. Even the optic mode alone has many facets.

2.1. Underwater camouflage. To begin with, the visual characteristics of animals are adaptively correlated with the environmental light pattern. While bottom living forms, such as flounder, camouflage themselves with colors and patterns which mimic the sandy or gravelly substrate, pelagic forms have several special strategies. One is shown by epipelagic gelatinous forms, like jelly fish, chaetognaths and salps, which become "invisible" by closely matching their optical properties to those of "empty" seawater itself. Reflection and absorption are strictly minimized and the refractive index closely approaches that of the medium. Hence the animals become highly transparent and glassy, a rather extraordinary feat for live, well differentiated creatures!

An alternative strategy feasible for larger and more complex animals is to match the optical properties of their body surface to the radiance distribution in the medium. Typically as in many fishes, such as tuna or mackerel, the dorsal surface is deeply pigmented in a Gulf Stream blue which matches in spectrum and intensity the feeble upwelling light around them. Laterally this pigment lightens to silvery sides and white belly which also closely fit the radiance surrounding them as observed from various directions. The optics of this system have been well studied by Eric Denton and J.A.C. Nicol at Plymouth[3], particularly with regard to the mirror-like lateral surfaces of herring and many other pelagic fish. These silvery reflectors provide an extraordinary method of closely simulating the natural radiance expected in a given line of sight if the fish were not there!

Ultimately, the fading of upwelling light as depth increases makes a passive system of this sort unable to eliminate the fish's shadow when it is observed from below (as by a predator). Denton again[1], supported in detail an earlier proposal that this shortcoming could be overcome in a variety of mesopelagic fishes by an active system in which the animal's shadow is eliminated by downwelling light generated by ventral and ventrolateral light organs as in the hatchet fish Sternoptyx and Argyropelecus. The bioluminescent spectrum modified by a blue filter or mirror in the photophores and the angular distribution of the light emitted match the properties required by the hypothesized shadow elimination. In addition the light intensity is continually adjusted to equal the natural downwelling radiance monitored visually by the fish[2]. Similar remarkable counter shading aided by ventral photophores have also been demonstrated in both mid-

water squid and shrimp[23]. Hence this extraordinary optical mechanism must have evolved independently at least three times! However, direct tests of its protective function in situ remain to be made'.

2.2. Vision and available light. Another area where multilayered interaction occurs between environmental optics and animal optics relates to eyes and to visual pigments which provide the molecular basis for seeing. These have to function effectively at the strongly attenuated irradiance levels available underwater and in limiting cases within the narrow band of wavelengths around 450-460nm which mark the maximum penetration of sunlight into the clearest ocean water. In general marine crustaceans and fish, particularly pelagic and mesopelagic forms, have the peak absorption of their visual pigments shifted towards shorter wavelengths compared with terrestrial and freshwater species. However, such a correlation has not been found in deepwater squids and their relatives.

Other things being equal such a blue shift would by itself sharply increase the visibility of penetrating sunlight in deep water or the maximum depth at which an animal can see. However, among several other elements in mesopelagic adaptation to dim light near the limits of vision, the considerable increase in the concentration of visual pigments found in the photoreceptor membranes of the retina considerably broadens the absorption curve. This would decrease the advantage to be gained from exactly tuning the visual pigment's λ_{max} to the absorption minimum of the water column to sunlight.

A factor in midwater vision competing with surface light is bioluminescence which apparently has many other uses beyond the counter shading just mentioned. Even around midday in the clearest ocean water the intensity of bioluminescence begins to exceed that of penetrating sunlight around 500m and becomes an increasingly prominent feature of underwater light down to 900m or so where the limits of the photic zone are being reached. Consequently tuning the spectral distribution of vision for bioluminescent communication, identification or pursuit at these depths becomes an important feature of animals' adaptation day and night. Typically pelagic bioluminescence as emitted has a λ_{max} between 450-490nm which corresponds roughly with the wavelengths of greatest transparency of seawater and the greatest sensitivity of resident animals' visual pigments.

A fascinating break with these generalities is found in certain predatory deepsea fish such as Malacosteus and Pachystomias which are conspicuous for having a red-peaking system apparently adapted for visual hunting and pursuit. This is invisible to most prey and other animals present. Consequently it would operate stealthily in the dark or near dark in some ways like a snooperscope. However, since the prospective prey do not emit red light, the Malacosteus system has to be an active one in which a large pair of subocular light organs illuminate nearby objects with light in a broad band around 700nm. As absorption losses to red light are high in sea water, ranges would presumably be limited to a few meters. The targets concerned, especially numerous mesopelagic shrimps which are deep red in color, reflect back the light to special long wavelength sensitive receptors in the predators' retinas. A deep red reflecting tapetum, also present in these eyes would sharpen the long wavelength channels. Generally undetectable "private" signalling between individual fish having the red system would also be quite possible.

3. UNDERWATER NAVIGATION

Interesting as these aspects of animal optics may be, a more difficult problem is raised by the question of whether vision underwater can contribute to the navigational needs for long range aquatic migrators. Many large fast swimming pelagic animals like sharks, billfish, tunas, salmon, eels, and whales regularly migrate hundreds or thousands of kilometers in their cyclic feeding and reproductive movements around the major oceans. It is a striking generality that all of these remarkable underwater navigators have well developed large eyes. Yet we know that visibility even in the clearest ocean water is several log units worse than in the atmosphere. In meteorological terms ranges of 50-200m correspond to a thick fog; yet a 200m visibility range is exceptional underwater. Landmarks could, of course, be used in the photic zone within these short sighting distances and very near the surface by profiles visible around the rim of Snell's window. However, this would account only for a trivial fraction of the habitat to be covered by pelagic migrators.

For humans visual piloting underwater is strictly short range for SCUBA divers and even submersibles for engineering or research. The Trieste, the Alvin and their sister ships, do of course, have observation ports or windows. Hence their navigators can see the bottom closeup or nearby reefs. Yet naval submarines lack them completely and once below periscope depth are quite blind. Despite their high speeds and long ranges, visual navigation is of no use to them after they are fully submerged. In its absence highly precise dead reckoning backed up by sophisticated echolocation and optical-electronic techniques provide the necessary courses and fixes. Most such instrumentation is clearly quite unavailable to marine animals!

How, then, should we interpret the fact that all long range oceanic migrators as mentioned have large well developed eyes? Even big whales, whose eyes are inconspicuous in their huge bulk, have the biggest eyes among mammals. It is also notable, for instance, that the common eel Anguilla on metamorphosis from the freshwater yellow eel into the ocean going silver eel develops much larger eyes and shifts the λ_{max} of its visual pigment towards the blue. Aside from rather close range detection of family members, prey or predators what are such well developed eyes for? Is it possible that they are essential for some aspects of oceanic navigation which are so far only speculative? What optical properties of marine light could be involved? The basic data an animal needs to navigate are location (map), direction (the compass) and time (the chronometer).

4. UNDERWATER LIGHT POLARIZATION

By definition, of course, the inherent optical characteristics of sea water would not provide navigational information. An exception might depend on some feature like a distinct change in the volume scattering function or the concentration of yellow substance which could serve to identify particular water masses for piloting. In contrast the underwater radiance distribution should provide direction information everywhere within the photic zone.

Indeed the 24h cycle of underwater radiance would also give a synchronizing time signal for an animal's chronometer, which is critical for starting, stopping or timing migratory movements. The typical situation is that internal clock mechanisms are basic to regulating all aspects of the organism's activity from enzyme or hormone synthesis to vertical migrations or reproduction. Yet because their free running period is only approximately 24h, their phase needs continual resetting by external signals to stay in step with environmental cycles.

Below the asymptotic depth, where penetrating light rays are symmetrical about the vertical even when the sun is on the horizon, the light distribution would not provide compass information. Nevertheless it could still serve as a vector parallel to gravity and hence a reliable clue for animal orientation in space somewhat like the dorsal light reflex. Above this asymptotic depth, which may be reached at 300-500m in clear ocean water, but is also wavelength dependent, there is an azimuth component in the underwater light distribution. Hence the radiance pattern can act as a compass except when the sun is in the zenith or the sky is uniformly overcast. The long axis of the ellipsoid describing the radiance distribution at a given depth and time will typically coincide with the directionality of the sun's rays underwater at the point of observation. The horizontal projection of that axis will give a continuous indication of the sun's bearing as long as it remains above the horizon.

Such a sun compass is well known in insects and birds as well as in fishes close to the water surface. Actually in shallow water and in a flat calm, the apparent location of the sun's disk can be readily observed within Snell's window. But with the usual disturbed surface conditions and with increasing depth Snell's window becomes distorted, indistinct and disappears; then the radiance distribution becomes a smooth ellipsoid. From a visual point of view the discrimination of the sun's bearing (or apparent elevation) becomes quite vague under such conditions. Consequently, a practical underwater sun compass for an animal requires some sensitive direct means of determining the orientation of the radiance distribution axis. Actually just such a mechanism has been known since 1954 when the author first described the basic pattern of underwater light polarization[12,14,15].

Interestingly the submarine polarization pattern basically depends on the same optical factor as the radiance distribution, namely the directionality of underwater light rays as observed from various directions. Whatever one's expectations might be, the selective reflection of the sun's rays at the surface has little influence on the ensuing pattern. Nor does the sun-dependent polarization of sky light have much effect except close to the surface during the day and within Snell's window where the sky may be observed directly. Refraction at the air water interface, of course, changes the direction of light and hence the observed e-vector orientation accordingly. As a result then the radiance ellipsoid provides an index to underwater polarization in any given plane. For instance, horizontally the distribution in a polar plot will be circular with the sun in the zenith or at or below the asymptotic depth when the sun is anywhere above the horizon. In any plane where the radiance distribution is elliptical, the minor axis will define e-vector direction and the difference between major and minor axes divided by their sum is the degree of polarization.

However, as stated, radiance distribution away from the near surface layers is a poor visual index for navigation. In contrast the e-vector direction can be rather accurately identified if the eye has a good polarization analyzer built in. Crustaceans (as well as insects and spiders) and cephalopods are well known to have more than one (usually two at 90°) dichroic channels in the retina highly sensitive to e-vector orientation. The fine structure of the photoreceptor membrane and the selective orientation of dichroic[16] visual pigment molecules are well known to be responsible for e-vector perception and related behavior. Such output functions are also rather well documented for fishes even though the mechanism of their analyzer has not yet been identified[6,17].

5. CURRENT RESEARCH PROGRAM

Given the underwater polarization pattern and the widespread ability of aquatic animals to sense the e-vector in light more than 10-20% polarized, we have been particularly interested in whether or not a visual compass based on these relations contributes to the navigation required to control the extensive migrations which occur in the sea. The orientation of e-vector is horizontal in the sun's (and the anti-sun's) bearing while its tilt from the horizontal is maximum (and facing toward the sun) at 90° to the solar azimuth. In the whole photic zone above the asymptotic depth, this solar compass is available to any of the animals that can read it. The compass use of sky polarization has been thoroughly documented for terrestrial animals particularly the honey bee and the desert ant[5,9,21]. Almost no comparable field work has been done on any aquatic organism. Indeed such experiments at sea are quite difficult even to conceive in view of the complex optics, poor visibility and long range behavior concerned. We tried some work of this sort in shallow water in Bermuda in the 1950's and in Palau in the 1970's but had problems in obtaining consistent results.

CLUPEA LARVAE (n=3615)

A — 16 Bins

B — 8 Bins

C — 4 Bins

D — 2 Bins

BEARING

NEOMYSIS (n=509)

A — 16 Bins

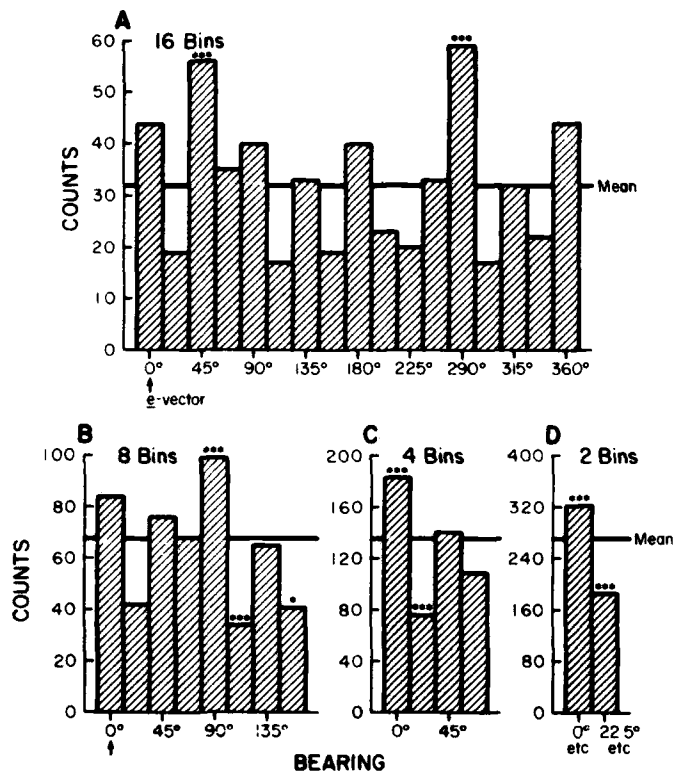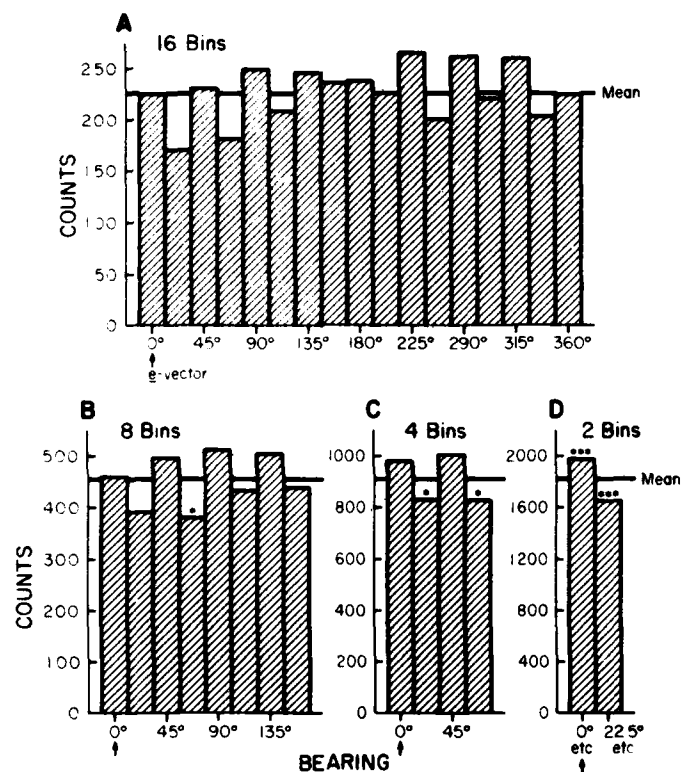**B** — 8 Bins

C — 4 Bins

D — 2 Bins

BEARING

Figure 1. Larval herring swimming in a field of downwelling linearly polarized light show spontaneous multiple peak preferred directions of azimuth orientation. These headings lie at 0°, 45°, 90° and 135° relative to the stimulus e-vector. Highly significant preference for these directions becomes clear in comparison with intermediate angles of 22.5°, 67.5°, etc. Original data were sorted into 16 22.5° bins around the circle (A), then folded into 180° (B), then 90° (C) and finally into two lots to compare 0°, 45°, etc. vs 22.5°, 67.5° etc. (D). Significant differences from a uniform distribution were evaluated by chi square, where * indicates p<0.05;**, p<0.01; and ***, p<0.001. This is the first demonstration of such multipeaked polarotaxis in fish.

Figure 2. Spontaneous directional orientation shown by adult shrimp-like Neomysis under conditions of experiment and analysis like those in Figure 1. Other species of crustaceans, as well as cephalopods and a number of kinds of insects, were previously known to orient selectively in a four peaked pattern (0°, 45°, 90° and 135°) relative to stimulus e-vector. The navigational importance of such behavior remains to be verified.

Our main concern at the moment is to improve the quality of relevant laboratory experiments and their analysis. A data reduction system which will step through video tape recordings of oriented behavior, viewed as spontaneous swimming in the horizontal plane, is nearly completed. This uses a VCR, frame advancer, Coreco frame grabber, and observer operated mouse to enter the x,y coordinates of the animal's successive positions in an IBM XT. A data analyzing program calculates directions and speeds for each time interval. These in turn are sorted into directional sectors and the resulting counts evaluated using chi-square. Preferred directions of azimuth orientation correlated with the experimental e-vector orientation, swimming rates and turning rates with and without polarization are all given in the summarizing printout.

Until that program is completed and the 30-40h of experimental tapes already recorded have been evaluated, sweeping conclusions are unwarranted. However, a brief presentation of our current work is appropriate here to provide some flavor of the research involved and its future projection. The experiments mostly on larval herring, and adult mysids, Neomysis, have been done over several years at the Dunstaffnage Marine Laboratory in Oban, Scotland with the generous collaboration of Dr. J.H.S. Blaxter and his associate Dr. Robert Batty. Spontaneous swimming behavior has been recorded under a variety of optical conditions relevant to a polarized light compass. Randomly sequenced e-vector azimuths of the downwelling stimulus light have been run against unpolarized controls. The amount of sidewelling light has been altered by using black or white surrounds. The latter would tend to mask any horizontal intensity differences due to selective scattering parallel and perpendicular to the e-vector. This has also been tested for with a surround made up of alternating black and white quadrants oriented relative to the polarization plane. In some experimental series an IR illumination and recording channel was used, independent of the polarized visible stimulating light.

For present purposes, two samples of the data obtained will illustrate their potential interest for animal navigation involving polarized light. They clearly demonstrate that both the shrimplike Neomysis and the herring larvae behave rather alike, despite their quite different kinds of eyes and remoteness in an evolutionary sense. The similarities involve two major points. Both animals swim differently in linearly polarized light than they do in unpolarized light. Both also show spontaneous compass card-like preferential directions at 45° intervals around 180° with an arbitrary 0° being set at 0° and 180° relative to the downwelling e-vector (Figs. 1 and 2).

Such compass card-like orientation to e-vector direction has been found before in crustaceans[7] and in cephalopods[8]. Yet this is the first time that fish have been shown to have multiple peaked preferences of this kind even though e-vector discrimination is known for several species. In general preferred orientation at 0°, 45°, 90° and 135° relative to a downwelling e-vector is most likely a response to experimental optical conditons quite remote from those normally experienced by the animals in the sea. After all neither human nor animal navigators ordinarily set their courses in eight directions simultaneously. Even so, such behavior is of considerable importance for two particular reasons.

To begin with patterned polarotactic responses of this sort no doubt reflect the underlying mechanism of e-vector perception and the ensuing oriented swimming. We know, for instance, that in both crustaceans and cephalopods the retina has two orthogonal dichroic input channels. This depends specifically on the precise microvillus fine structure of the photoreceptor membrane. Thus the multipeaked orientation response with a 45° period suggests that a differential turning tendency leads to orientation in directions where the difference curve for the two channel input has zero slope. However, the fact that herring larvae have polarotactic patterns closely similar to those of crustaceans and cephalopods does not obviously allow the same explanation. Microvilli and rhabdoms are not present in vertebrate eyes. Hence their demonstrated sensitivity to e-vector direction must arise from a different mechanism.

Some recent conditioned reflex experiments with goldfish do indeed suggest that there are two cone types differentially sensitive to both wavelength and 90° e-vector orientation[6]. Actually no fine structural evidence exists for two operationally dichroic kinds of cone in fish retinas except uniquely in the anchovy[4] for which critical experiments are still lacking. Actually earlier research using intra-cellular recordings from the optic tectum has demonstrated e-vector discrimination in the goldfish[18,19]. Yet no evidence was found for two discrete e-vector sensing channels. Clearly further research is needed to explain these apparent discrepancies. However, the navigational implications of polarotactic behavior, rather than its sensory mechanisms, are more directly related to our interest here.

In that context the multiple peak orientation currently being observed in mysids and fish might be thought of as expressing some sort of idling behavior in the course steering mechanism mediated by underwater polarized light. To engage this system either some more realistic simulation of the natural light in the sea or a way of motivating or providing a goal for the experimental animals must be found. Consequently a major item on the agenda is to construct and test the Stachnik simulator described in the preceding paper[10,11]. By providing polarized side welling, as well as upwelling, illumination in the experimental vessel, this will more closely mimic natural underwater light than has been possible in the laboratory before. On the basis of many earlier findings, important behavior patterns not previously accessible to study may well be expressed under such new conditions.

Another aspect of multiple peak responses to polarized light also deserves further research. This relates to the notion recently emphasized by Wehner[21] that the functional organization of a receptor system may act as a filter or template in processing complex input signals. This could bypass sophisticated

calculations and insights required for an analytical solution. Such a template-like device seemed appropriate in accounting for the elegant data[22] on compass orientation by honey bee workers using sky polarization. In essence the bilateral fanshaped distribution of dichroic photoreceptors in the specialized dorsal margin of their compound eyes is considered an optical template for sky navigation. It has to be matched against a simplified map-like distribution of sky light $\underline{e}$-vectors. Maximum response should be obtained in the model proposed when the bee's heading coincides with the sun's bearing (whether or not the latter is visible).

A somewhat comparable template mechanism dependent on the 90° two channel $\underline{e}$-vector sensing system of crustaceans and cephalopods was proposed many years ago to explain multipeaked polarotactic responses[13,20]. The inputs of each retinal unit of such a system would vary as $\cos^2 \zeta$ for one channel and $\sin^2 \zeta$ for the other where ζ is the $\underline{e}$-vector orientation. Adding these two channels would yield an overall intensity measure while subtracting or multiplying the inputs could provide turning forces for multiple peak orientation like that in the current data. Renewed research and analysis from this point of view should yield important results relating to spatial orientation, station keeping, and compass functions needed for navigation.

6. CONCLUSIONS

Polarized light underwater offers animals able to use it, visual reference for spatial orientation, to the otherwise absent horizon, anywhere in the photic zone. Above the asymptotic depth the polarization pattern will also indicate the sun's bearing, a common reference for shallow water and terrestrial animal compasses. Current laboratory experiments add herring larvae and mysids to the crustaceans and cephalopods previously known to orient in a stereotyped way to a downwelling $\underline{e}$-vector. How a useful course heading is generated from this reaction remains to be discovered.

7. ACKNOWLEDGMENTS

8. REFERENCES

1. Denton, E.J., J.B. Gilpin-Brown and P.G. Wright. The angular distribution of the light produced by some mesopelagic fish in relation to their camouflage. Proc. R. Soc. Lond. B. 182:145-158. 1972.
2. Denton, E.J., P.J. Herring, E.A. Widder, M.F. Latz and J.F. Case. The roles of filters in the photophores of oceanic animals and their relation to vision in the ocean. Proc. R. Soc. Lond. B. 225:63-97. 1985.
3. Denton, E.J., and J.A.C. Nicol. A survey of reflectivity in silvery teleosts. J. Mar. Biol. Assoc. U.K. 45:685-722. 1966.
4. Fineran, B.A. and J.A.C. Nicol. Novel cones in the retina of the anchovy (Anchoa). J. Ultrastruct. Res. 541:296-303. 1978.
   von Frisch, K. Tanzsprache und Orientierung der Bienen. Springer-Verlag, Berlin, Heidelberg, New York. 578pp. 1965.
6. Hawryshyn, C.W. and W.N. McFarland. Cone photoreceptor mechanisms and the detection of polarized light in fish. J. Comp. Physiol. A 160:459-465. 1987.
7. Jander, R. and T.H. Waterman. Sensory discrimination between polarized light and light intensity patterns by arthropods. J. Cell. Comp. Physiol. 56:137-160. 1960.
8. Jander, R., K. Daumer and T.H. Waterman. Polarized light orientation by two Hawaiian decapod cephalopods. Z. Vergl. Physiol. 46:383-394. 1963.
9. Rossel, S. and R. Wehner. Polarization vision in bees. Nature 323:128-131. 1986.
10. Stachnik, W.J. The simulation of marine light fields including polarization and the related visual behavior of Mysidopsis. Ph.D. Thesis, Yale University. 352pp. 1986.
11. Stachnik, W.J. The physical simulation of marine light fields for marine animal visually mediated behavior in investigations. Ocean Optics IX. 1988.
12. Waterman, T.H. Polarization patterns in submarine illumination. Science 120:927-932. 1954.
13. Waterman, T.H. Systems analysis and the visual orientation of animals. Am. Sci. 54:14-45. 1966.
14. Waterman, T.H. Underwater light and the orientation of animals. In: Optical Aspects of Oceanography. N.G. Jerlov, E. Steemann Nielsen, eds. Academic Press, London. pp. 415-443. 1974.
15. Waterman, T.H. Natural polarized light and $\underline{e}$-vector discrimination by vertebrates. In: Light as an Ecological Factor: II. G.C. Evans, R. Bainbridge and O. Rackham, eds. Blackwell Scientific Publications. Oxford. pp. 305-335. 1975.
16. Waterman, T.H. Polarization sensitivity. In: Handbook of Sensory Physiology, Vol. VII/6B. H. Autrum, ed. Springer-Verlag, Heidelberg, Berlin, New York. pp. 291-469. 1981.
17. Waterman, T.H. Natural polarized light and vision. In: Photoreception and Vision in Invertebrates. M.A. Ali, ed. Plenum Press, New York. pp. 63-114. 1984.
18. Waterman, T.H. and K. Aoki. E-vector sensitivity patterns in the goldfish optic tectum. J. Comp. Physiol. 95:13-27. 1974.
19. Waterman, T.H. and H. Hashimoto. E-vector discrimination by the goldfish optic tectum. J. Comp.

Physiol. 95:1-12. 1974.

20. Waterman, T.H. and K.W. Horch. Mechanisms of polarized light perception. Science 154:467-475. 1966.

21. Wehner, R. "Matched filters" - neural models of the external world. J. Comp. Physiol. 161:511-531. 1987.

22. Wehner, R. and S. Rossel. The bee's celestial compass - a case study of behavioural neurobiology. Fortschr. Zool. 31:11-53. 1985.

23. Young, R.E. and C.F.E. Roper. Intensity regulation of bioluminescence during countershading in living midwater animals. Fish. Bull. U.S. 75:239-252. 1977.